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Interannual Variability in American Lobster Settlement: Correlations with Sea Surface Temperature, Wind Stress and River Discharge

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**INTERANNUAL VARIABILITY IN AMERICAN LOBSTER SETTLEMENT:
CORRELATIONS WITH SEA SURFACE TEMPERATURE,
WIND STRESS AND RIVER DISCHARGE**

By

Mahima Jaini

B.S. University of Maine, 2008

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Marine Biology)

The Graduate School

The University of Maine

May, 2011

Advisory Committee:

Richard Wahle, Research Associate Professor, School of Marine Sciences, Advisor

Andrew Thomas, Professor, School of Marine Sciences

Andrew Pershing, Research Associate Professor, School of Marine Sciences

Robert Steneck, Professor, School of Marine Sciences

THESIS ACCEPTANCE STATEMENT

On behalf of the Graduate Committee for Mahima Jaini, I affirm that this manuscript is the final and accepted thesis. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

Richard Wahle, Research Associate Professor

Date

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By Mahima Jaini

Thesis Advisor: Dr. Richard Wahle

An Abstract of the Thesis Presented
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Recruitment to benthic marine populations is fundamentally a biophysical problem. The American Lobster Settlement Index is an annual diver-based survey of the young-of-year American lobsters (*Homarus americanus*) found in inshore nurseries in New England, USA and Atlantic Canada at the end of the postlarval settlement season. The considerable interannual variability in the settlement index suggests that environmental factors play an important role in regulating planktonic larval supply and transport. In this study, I focused on the longest settlement time series from three oceanographically contrasting regions: Midcoast Maine, coastal Rhode Island and the lower Bay of Fundy. Sampling in these regions was initiated in 1989, 1990 and 1991, respectively. I evaluated the correlation of inshore lobster settlement with sea surface temperature time series from satellites; wind data from buoys and land stations; and river discharge data from inland gauge stations. Correlations were performed between the annual lobster settlement indices and the monthly environmental metric with time lags up to three months prior to the month of settlement sampling, just before larvae hatch into the water column.

Interannual variability in lobster settlement correlated strongly with SSTa and wind stress, but exhibited a weak association with river discharge. Statistically significant correlations were restricted to the two-month window when larvae and postlarvae are in the water column. Correlations of the settlement index with monthly satellite-derived sea surface temperature anomalies (SSTa) mapped to recognizable features on the sea surface. For example, the Rhode Island lobster settlement index correlated positively with SSTa found over Georges Bank up to two months prior to settlement sampling. Rhode Island settlement index also correlated with alongshore component of wind stress over Georges Bank for the month of settlement sampling. Midcoast Maine lobster settlement correlated weakly with sea surface temperature anomalies, but a strong positive correlation was found with alongshore wind stress during the month prior to settlement sampling. Only Midcoast Maine lobster settlement showed a negative association with local monthly river discharge. Bay of Fundy lobster settlement was positively correlated with sea surface temperature anomalies and cross-shore wind stress at two of the closest wind stations, one month prior to settlement sampling.

In short, sea surface temperature anomalies and wind stress proved to be strong environmental correlates of lobster settlement in this analysis. All significant relationships consistently fell within two months of the settlement sampling, a time when larvae and postlarvae occupy the water column. These results suggest satellite SSTa data and wind data from multiple stations may be useful in predicting interannual fluctuations in lobster settlement, and therefore may lead to a better understanding of the mechanisms influencing recruitment variability.

ACKNOWLEDGEMENTS

I would like to thank my advisors, Dr. Richard Wahle and Dr. Andrew Thomas for their help with planning and executing this study. They managed to take time out to meet with me to discuss statistical and theoretical issues, and went through numerous drafts of this thesis. I would also like to thank the rest of my committee members, Dr. Andrew Pershing and Dr. Robert Steneck, for their continuous support and oversight in the project. Ryan Weatherbee provided immense amount of support in the data analysis. Dr. Lew Incze and Dr. Huijie Xue provided a fresh perspective on the results. Thank you all.

I would also like to acknowledge all the agencies behind the data; the American Lobster Settlement Index Collaborative, the Satellite Oceanography Lab at UMaine, National Aeronautics and Space Administration, National Data Buoy Center, Canadian Department of Fisheries and Oceans, United States Geological Survey and the Weather Survey of Canada and the many people that have been involved in collection of it. Without you this work would not have been possible.

Funding for my graduate work came from Teaching Assistant (TA) positions and the graduate student fellowship at the School of Marine Sciences (SMS). I would like to thank Dr. Kevin Eckelbarger, Dr. Robert Steneck, Dr. Mary Jane Perry, Dr. Emmanuel Boss and Dr. Pete Jumars for taking me on as their TA on multiple occasions. They have taught me an immense deal about patience and humility. I would also like to thanks Dr. William Ellis, Sue Thibodeau, Jessie Gunning, Jodie Feero, Sarah Joughin and Mireille Le Gal for their help with my various financial and official requirements. I am greatly in

debt to SMS and the Office of International Programs for their support throughout my undergraduate and graduate years.

Last but not least, I'd like to thank my family and friends around the world that have supported me throughout my schooling, even when they didn't exactly understand what I was doing. I would like to thank my fellow graduate students, housemates, and friends for listening to my thesis rants, my parents for always supporting my interests and letting me travel the world in pursuit of them, and my sister for always encouraging me to do better.

Thank you for all the love and kindness you have shown me!

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1. INTRODUCTION

Recruitment to benthic marine populations is fundamentally a biophysical problem involving key biological factors that affect egg production and key physical oceanographic factors that influence the survival and transport of the pelagic propagules to suitable nursery grounds. This study examines the environmental correlates of interannual variability in postlarval settlement of the American lobster (*Homarus americanus* H. Milne Edwards, 1837) in Gulf of Maine and southern New England Shelf waters. Here I evaluate the correlation of inshore lobster settlement with sea surface temperature data from satellites, wind data from buoys and land stations, and river discharge data from inland gauge stations. Of interest are consistent ocean environmental metrics that may be useful to predicting interannual variability in lobster settlement at coastal monitoring sites.

Satellites provide high-resolution spatial and temporal coverage of many oceanographic variables such as temperature, chlorophyll, wind and sea surface height, and thus have been used in studies of biological recruitment, population connectivity and fisheries oceanography. One of the very first studies utilizing satellite-derived sea surface temperature (SST) data to examine the impact of coastal upwelling on barnacle (*Balanus glandula*) settlement dates back to 1988 (Roughgarden et al. 1988). Subsequent studies have linked satellite-derived indices of upwelling and onshore retention to recruitment of commercially important species such as *Concholepas concholepas* (Moreno et al. 1998), *Octopus vulgaris* (Demarcq and Faure 2000), *Trachurus trachurus* (Santos et al. 2001),

Sardinops sagax and *Engraulis capensis* (Cole 1999, Hardman-Mountford et al. 2003). Larval *Melanogrammus aeglefinus* survival was shown to be dependent on the timing of the spring bloom as revealed by satellite chlorophyll (Chl) data (Platt et al. 2003). Similarly, reef fish recruitment has been related to larval delivery by frontal eddies detected in SST and Chl satellite images (Sponaugle et al. 2005). Satellite-derived sea surface height has been used to model currents and larval transport of spiny lobsters (*Panulirus marginatus*: Polovina et al. 1999, *Jasus edwardsii*: Chiswell and Booth 2008). Although these studies shed light on phenomena that would not have been identified without the use of satellite imagery, few have quantified direct relationships between satellite derived data and marine biological recruitment. Caputi et al. (2001) found a positive correlation between *Panulirus cygnus* settlement in inshore grounds and the satellite-derived SST averaged over the region of the warm Leeuwin current where their phyllosoma larvae are known to occur. Broitman et al. (2008) found regional differences in links between settlement in *Balanus glandula* and *Mytilus* spp. and satellite-derived local SST; the direct link being stronger along the coast of Oregon than off California. This thesis is the first to evaluate large-scale spatial associations between interannual variability in lobster settlement and satellite-derived SST anomalies over regions relevant to lobster larval supply and transport.

The American lobster fishing industry in the US and Canada is valued at about one billion US dollars (FAO 2008). It constitutes the largest lobster fishery in the world (Wahle et al., in press). Sustainability of this fishery depends on adequate recruitment of lobsters to fished populations. Fishery recruitment in most areas is dependent on the

successful recruitment of early benthic phase lobsters (Fogarty and Idoine 1986, Steneck and Wilson 2001). Year class strength varies in time and space, largely depending on the pelagic larval supply (Incze and Wahle 1991, Incze et al. 1997, Incze et al. 2000). With a 3-12 week pelagic phase (Ennis 1995), American lobster larvae are under the influence of a multitude of environmental factors that affect their transport and subsequent recruitment to nursery habitats. Here I evaluate annual lobster settlement in relation to temperature, wind and freshwater discharge, as past studies have linked these variables to lobster biology, larval development, behavior, transport, settlement and even fisheries landings (See Section 2. Background). I use data from the American Lobster Settlement Index, an annual diver-based survey conducted at more than seventy sites along the coast of New England and Atlantic Canada. The index is an annual metric of the biological recruitment of young-of-year lobsters to monitoring sites at the end of the larval settlement season in the late summer - early autumn. For this study I am focusing on the longest settlement index time series from three oceanographically distinct regions; Midcoast Maine initiated in 1989, coastal Rhode Island initiated in 1990 and lower Bay of Fundy initiated in 1991 (Figure 2 and 3).

The main objective of this study is to investigate the correlation of American lobster settlement with easily accessible and measurable metrics of environmental variability. Satellite data enable an evaluation of the spatial scale of the association. Since lobster larvae spend anywhere from 3 – 12 weeks in the plankton depending on temperature (Ennis 1995, Annis et al. 2007), the influence of the environmental variable under consideration may vary depending on the larval stage and timing. Monthly averages of

the environmental variables are used to assess lagged relationships up to three months prior to the settlement sampling. The use of three oceanographically distinct settlement regions helps us to identify regionally specific differences in these spatial and temporal associations. Although the emphasis is the identification of ocean features that may be useful in forecasting time trends in lobster settlement, I also explore plausible mechanisms behind observed associations with hope to better understand the sources of settlement variability.

2. BACKGROUND

2.1 AMERICAN LOBSTER SETTLEMENT

The American lobster has a biphasic life cycle, with pelagic larval and postlarval phases and benthic juvenile and adult phases (Figure 1). Settlement marks the transition from pelagic to a benthic form of existence. American lobster larvae hatch into the water column from early to mid-summer. They undergo three larval zoeal instars and then metamorphose into a postlarval megalopal instar (Factor 1995, Figure 1). Postlarvae actively seek shelter-providing benthic habitat, such as cobble beds, for settling. The pelagic phase usually lasts between 3 – 12 weeks (Ennis 1995).

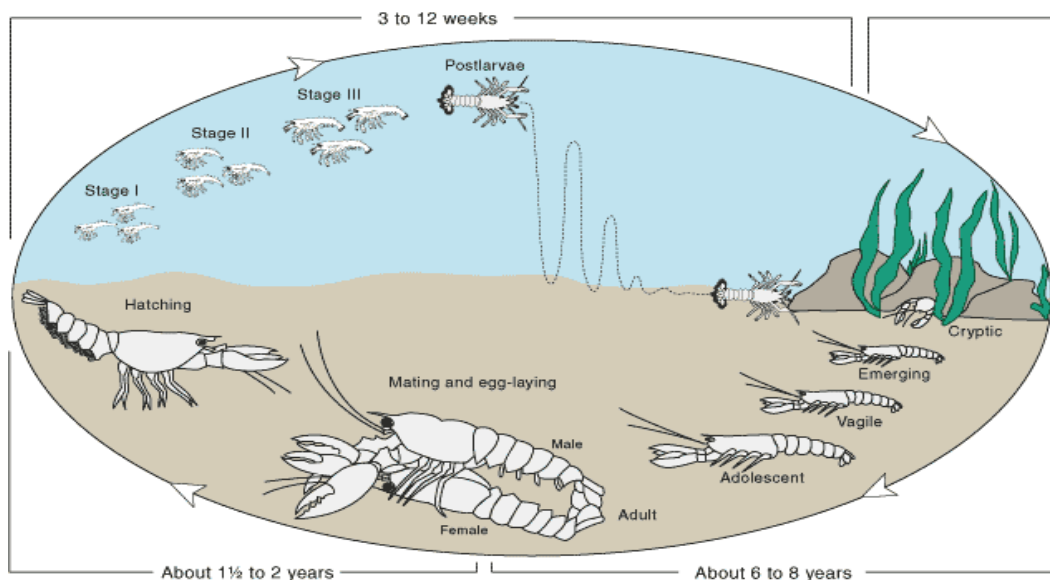


Figure 1. American lobster life cycle. (Source: St. Lawrence Global Observatory – SLGO, <http://slgo.ca/>, 2011)

Successful settlement is a function of all the events prior to it (Figure 1). Interannual variability in American lobster settlement could stem from variability in egg production, larval hatching, development, survival and transport. The broodstock size for the Gulf of Maine and Georges Bank has remained at healthy levels for the past twenty years but the southern New England region has shown a dramatic decline in lobster abundance over the past decade (ASMFC 2009). Although decadal trends in the abundance of broodstock are evident for all regions, there is relatively little interannual variability owing to the long life and conservation of breeding females (ASMFC 2009). Environmental factors, however, such as temperature and oxygen availability can affect egg development and survival (Factor 1995). Warming bottom temperatures stimulate egg development and trigger hatching (Fogarty 1983, Aiken and Waddy 1986, Cobb and Wahle 1994, Ennis 1995), thus variability in onset of spring warming could affect timing of hatch. Larval development and growth are faster in warmer water (Templeman 1936, Hudon and Fradette 1988, Ennis 1995, Annis et al. 2007). The vagaries of larval transport can give rise to dramatic variation in the larval supply to shallow coastal nurseries. As plankton, lobster larvae are transported by wind driven-currents and circulation at small and large scales (Harding and Trites 1988, Hudon and Fradette 1993, Wahle and Incze 1997, Xue et al. 2008). Additionally, behavioral responses to temperature (Harding et al. 1987, Boudreau et al. 1991, Boudreau et al. 1992, Annis 2004, Annis 2005) and salinity (Templeman et al. 1936, Sastry and Vargo 1977, Scaratt and Raine 1967) thresholds can affect the distribution of larvae in the water column and thus their subsequent transport.

A link between temperature and settlement has been suggested for both US and Canadian waters by correlations between lobster landings and temperature fluctuations time lagged by six to eight years, the average time young-of-year lobsters would need to grow to harvestable size (Dow 1969, Flowers and Saila 1972, Boudreault et al. 1977, Dow 1977, Dow 1978, Steneck 2005). Similarly, wind (Boudreau et al. 1991) and river discharge (Sutcliffe 1972 and 1973) have also been found to correlate with lobster landings lagged by six to eight years, but only for the Gulf of St. Lawrence. The more recent ability to monitor settlement itself has permitted a more direct assessment of the role of processes influencing young-of-year recruitment, as is shown here.

2.2 PHYSICAL SETTING

The lobster settlement monitoring locations used in this study span a dramatic gradient in oceanographic conditions along the New England coast and continental shelf (Figure 2 and 3). During the summer months, the southern New England Shelf and southwestern Gulf of Maine become thermally stratified, whereas the eastern Gulf of Maine and Bay of Fundy remain well mixed by the extreme tides of the region (Figure 2 and 3). Seaward of Georges Bank (see Figure 2) is the region of confluence between warm Gulf Stream waters coming from the south and cold Labrador Current waters coming from the north, making it an area of high SST variability (Townsend et al. 2006).

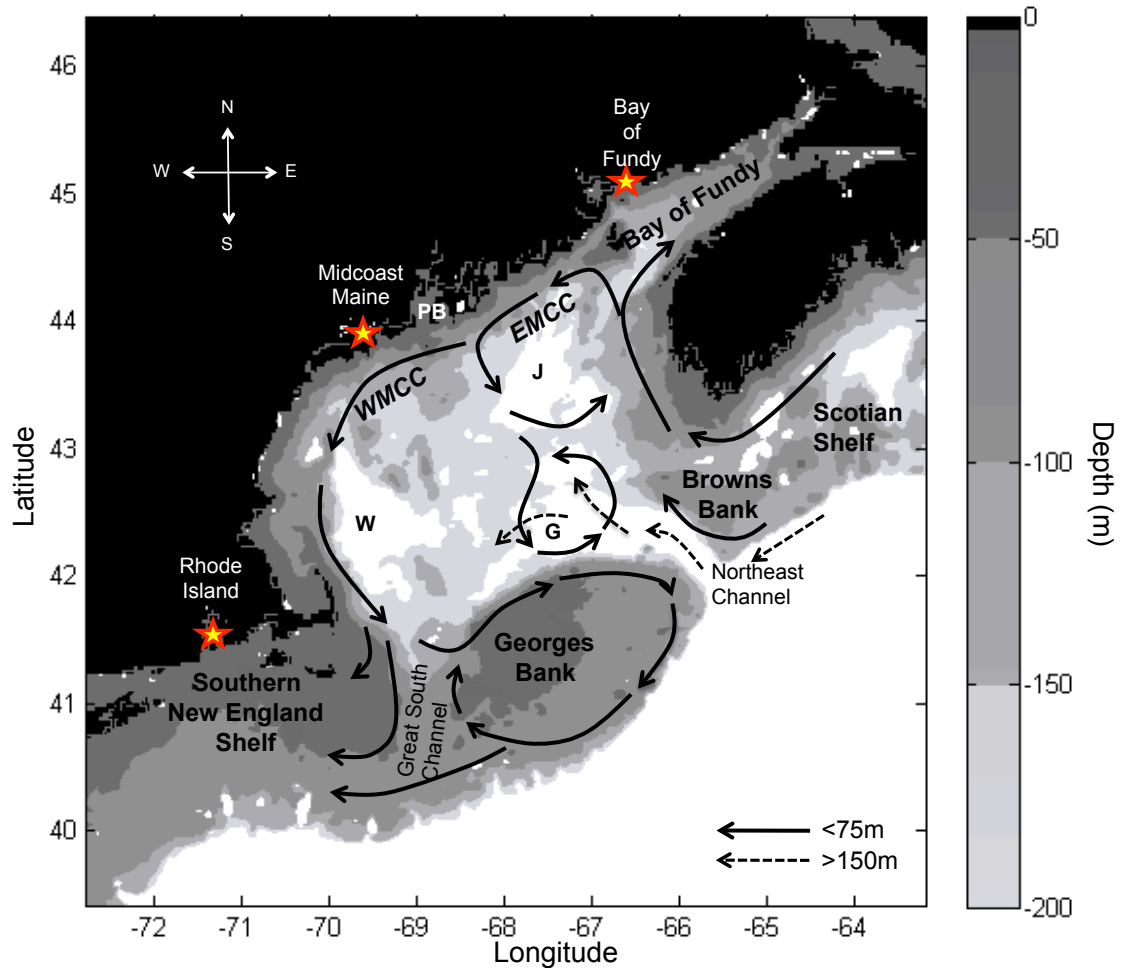


Figure 2. Oceanography of the Gulf of Maine and neighboring shelf areas showing the prominent oceanographic features and general surface (<75m) circulation patterns. Stars indicate the sampling locations of the American lobster settlement regions used in this study (From N to S: Bay of Fundy, Midcoast Maine and Rhode Island). White areas are deeper than 200m. Deep circulation (>150m) shows the entry of deep Slope Water into the Gulf of Maine through the Northeast Channel. (EMCC=Eastern Maine Coastal Current, WMCC=Western Maine Coastal Current, PB=Penobscot Bay, W=Wilkinson Basin, J=Jordan Basin, G=Georges Basin).

One of the main oceanographic features in the Gulf of Maine is the Gulf of Maine Coastal Current, a near-surface, pressure-driven, cyclonic circulation that flows from east to west along the coast. This current is driven by density contrasts set up by dense Slope Water found in the deep basins that enters the Gulf of Maine through the Northeast

Channel and low salinity Scotian Shelf Water that enters the gulf over the Scotian Shelf and river discharges from the St. John, Penobscot, Kennebec/Androscoggin and Merrimac Rivers (Figure 2, Townsend et al. 2006). The coastal current has two components. The Eastern Maine Coastal Current is the stronger of the two, reaching speeds of $15 - 30 \text{ cm s}^{-1}$. It often bifurcates at the mouth of the Penobscot Bay either veering offshore and dissipating over the deep waters of the Gulf, or continuing along the coast as the Western Maine Coastal Current, at somewhat reduced speeds of $5 - 15 \text{ cm s}^{-1}$ (Figure 2, Pettigrew et al. 2005). If the bifurcation at Penobscot Bay is weak, the Western Maine Coastal Current can continue to flow along the coast of the western Gulf of Maine until it reaches Cape Cod, where it either gets entrained in the anticyclonic circulation over Georges Bank or flows out into the southern New England Shelf at the Great South Channel (Figure 2). Georges Bank is a shallow ($<100 \text{ m}$) submerged terminal glacial moraine where upwelling of deep water mixes to the surface at the northern flank (Figure 3, Townsend et al. 2006). Upwelling is also observed in the Great South Channel (Figure 3, Townsend et al. 2006). Manning et al. 2009 reported current speeds between $20 - 29 \text{ cm s}^{-1}$ on the northern flanks and $15 - 24 \text{ cm s}^{-1}$ on the southern flanks of Georges Bank.

Circulation variability in the Gulf of Maine is driven by wind forcing and changes in density structure due to entering deep Slope Water, Scotian Shelf Water or freshwater discharge from rivers (Smith et al. 2001, Pettigrew et al. 2005, Pringle 2006). The offshore veering of the Eastern Maine Coastal Current is associated with the Penobscot outflow and the transition from the tidally well-mixed eastern shelf to the more vertically stratified western shelf (Pettigrew and Xue 2006). Winds from the northeast accelerate

the flow of the Gulf of Maine Coastal Current to the southwest and help maintain connectivity with the western Gulf of Maine (Pettigrew and Xue 2006). SST has been shown to be an important tracer of the cold Eastern Maine Coastal Current (Figure 3, Bisagni et al. 1996, Pettigrew et al. 1998). Principal component analyses of satellite SST images highlights differences between east – west and inshore – offshore regions of the Gulf of Maine, and also reveal the spatial structure of circulation over the eastern Maine Shelf and Georges Bank (Figure 3, Bisagni et al. 2001). Using satellite-derived SST and Chl images one can observe differences in coastal waters, Georges Bank, Scotian Shelf and Nantucket Sound (Fox et al. 2005). On the other hand, southern New England Shelf waters show strong stratification throughout the summer months (Figure 3, Wilkin 2001, Codiga and Ullman 2010), and are influenced by circulation from the Georges Bank and Great South Channel (Manning et al. 2009).

Thus, oceanographic variability, as measured by variability in SST, winds or river discharge, over the Gulf of Maine, Scotian Shelf, Georges Bank and southern New England Shelf, can have an impact on lobster settlement in the inshore nursery grounds of concern here. But variability in off shelf regions that are under the influence of the Gulf Stream is probably not related to inshore lobster settlement for our study regions.

3. DATA AND METHODS

3.1 AMERICAN LOBSTER SETTLEMENT INDEX

The American Lobster Settlement Index is a collaborative annual survey by state and provincial marine resource agencies in the Northeast US and Atlantic Canada, respectively (Wahle et al. 2010). Initiated in 1989, the survey employs diver-based suction sampling (Wahle and Steneck 1991; Incze and Wahle 1991) and more recently, vessel-deployed passive postlarval collectors (Wahle et al. 2009) to assess settlement of American lobsters to inshore cobble nursery grounds at the end of the late summer-early autumn postlarval settlement season (Wahle et al. 2010). Some 70 fixed sampling sites are subdivided into 13 regional sets of 5-10 sites that are sampled annually. At each site twelve 0.5 m² quadrats are sampled by suction sampling (Table 1). The month of sampling and size definition of young-of-year settled lobsters varies by region because of temperature dependent differences in the hatching times and growth rates (Table 1). Sites within the region are averaged to a regional mean lobster settlement density with associated statistics such as standard deviation and standard error.

For the present analysis I used lobster settlement time series available through 2008 from three regions: Midcoast Maine, USA comprised of eight sites initiated in 1989; Rhode Island, USA, initiated with two sites in 1990 and expanded to six sites by 1993; and Beaver Harbour, NB, Canada, initiated with two sites in 1991, expanded to four by 1992

and five by 2007. In this study Beaver Harbour region is referred to as the Bay of Fundy region.

Table 1. American Lobster Settlement Index (ALSI) sampling details by study region.

Region	Latitude	Longitude	Years Analyzed	Sampling month	YoY size	Approx. area	# of sites
Bay of Fundy	44°58'12"N	66°48'36"W	1991-2008	October	≤ 13 mm	250 km ²	2 to 5
Midcoast Maine	43°45'36"N	69°31'12"W	1989-2008	September	≤ 10.5 mm	500 km ²	8
Rhode Island	41°25'12"N	71°18'00"W	1990-2008	August	≤ 13 mm	500 km ²	2 to 6

3.2 SEA SURFACE TEMPERATURE

Satellite-derived sea surface temperature (SST) images provided comprehensive spatial and temporal coverage of our study area for the time period of the lobster settlement index. The satellite SST data came from two sources: a New England NOAA AVHRR (Advanced Very High Resolution Radiometer) Pathfinder product (1985-1997) and a locally received and processed AVHRR SST product (1998-2008). The Pathfinder dataset was developed by the University of Rhode Island's Graduate School of Oceanography from four images per day and processed to SST using the Pathfinder protocol (Ullman and Cornillon 1999) and cloud-masking approach of Cayula and Cornillon (1996). These data were subset to geographical limits of 41.5 – 45° N and 66 – 71 ° W, archived and used to calculate monthly composites (average of all available images for that month) by the Satellite Oceanography Laboratory at the University of Maine's School of Marine Sciences (Thomas et al. 2010). The locally received AVHRR data were acquired directly by the Terascan receiving system at the University of Maine.

The 4-6 images received per day were processed into SST images using standard NOAA coefficients and customized cloud-masking techniques (Luerssen et al. 2005) modeled after the Cayula and Cornillon (1996) approach. Daily images were averaged to form monthly composites at a ~ 1.1 km spatial resolution. For the time period of overlap (1998), the two satellite SST sources correlated strongly (Luerssen et al. 2005). There was also significant ($p < 0.05$) agreement between monthly SST composites derived from buoys and spatially averaged satellite fields over areas of 1, 25 and 100 km² surrounding the focal buoy location (Appendix A).

Satellite SST composites for each month were averaged for the time period (1985-2008) to produce monthly climatologies (see example of climatology images in Figure 3). Monthly SST anomaly (SSTa) images were calculated as deviations of monthly composites for a particular year from the monthly climatology. As these anomalies highlight interannual variability in SST, in this study we used monthly SSTa images for the summer and fall months (May through October) over the length of the lobster settlement time series (1989-2008) to explore relationships between settlement and SST.

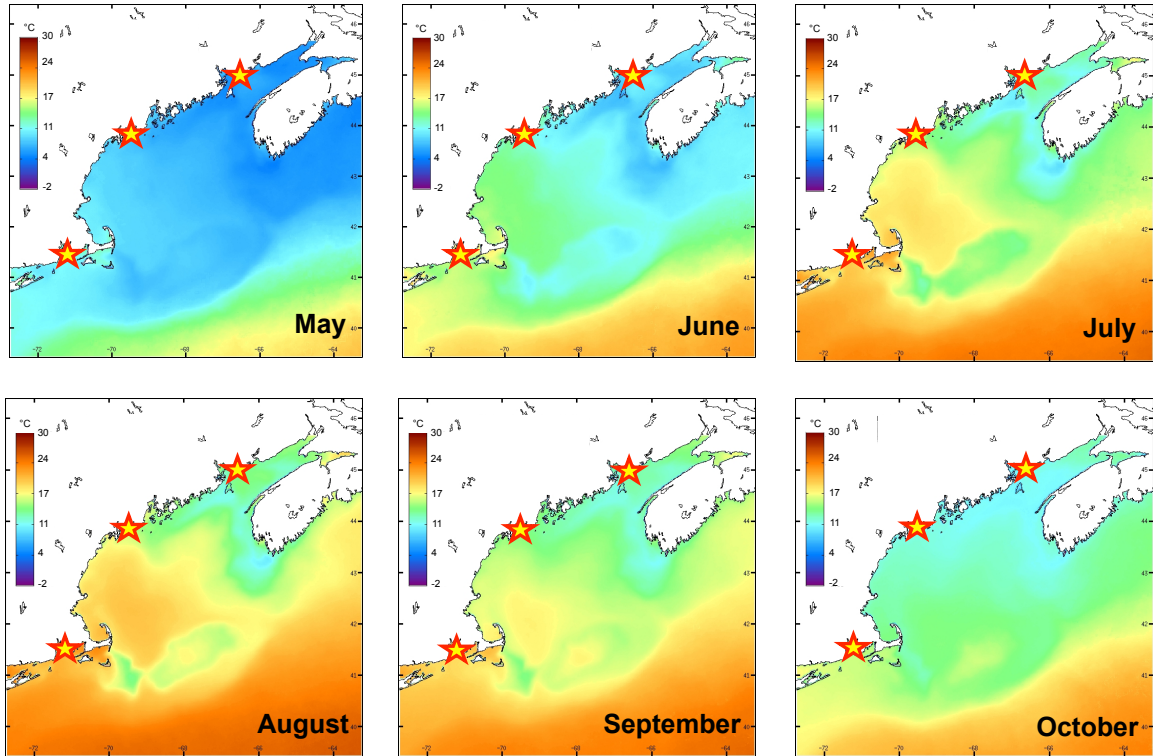


Figure 3. Monthly SST climatologies (1985 – 2010) from early summer through fall highlighting spatial differences in SST patterns for the three study regions indicated by stars. The cold Eastern Maine Coastal Current can be seen against the warmer surface waters of the Gulf of Maine. Upwelling of cold water over Georges Bank and the Great South Channel is also visible. (Source: UMaine Satellite Oceanography Lab)

3.3 WIND

Multiple buoy and island meteorological stations provided time series of wind vectors over the study period for analysis of relationships between lobster settlement and wind forcing. Alongshore and cross-shore components of wind stress were calculated for comparison to the lobster settlement time series, as these drive Ekman transport of the surface ocean.

Hourly wind speed (w) and wind direction (θ) data, for the Gulf of Maine and neighboring shelf areas, were obtained from National Data Buoy Center (NDBC) buoys and island stations (NDBC, <http://www.ndbc.noaa.gov/>) and Canadian weather station at St. John, New Brunswick (Department of Fisheries and Oceans: Atlantic Zone Monitoring Program, <http://www.dfo-mpo.gc.ca/>) (Figure 4, Table 2). These parameters were used to calculate daily alongshore (from the southwest) and cross-shore (from the southeast) wind velocity components (Figure 5 and 6). The coastal orientation (CO) differed only slightly from region to region, thus CO was taken to be 25° anticlockwise from true east (Figure 6). Daily alongshore and cross-shore winds were used to calculate monthly average alongshore stress (τ_a) and cross-shore stress (τ_x) in units of N m^{-2} (Figure 5 and 6).

Table 2. Station details for sources of wind data. (GoM = Gulf of Maine, SNE = Southern New England, NDBC = National Data Buoy Center, DFO = Department of Fisheries and Oceans).

Station	Location	Type	Latitude	Longitude	Anemometer height above sealevel	Source
44007	Portland ME, W GoM	Buoy	43°31'53"N	70°08'39"W	5 m	NDBC
44008	SW corner Georges Bank	Buoy	40°30'09"N	69°14'48"W	5 m	NDBC
44011	NE corner Georges Bank	Buoy	41°07'06"N	66°34'42"W	5 m	NDBC
BUZM3	Buzzards bay MA, SNE	Buoy	41°23'48"N	71°02'00"W	24.8 m	NDBC
MDRM1	Mount Desert Rock ME, E GoM	Island Station	43°58'06"N	68°07'42"W	31.7 m	NDBC
MISM1	Matinicus Rock ME, GoM	Island Station	43°47'00"N	68°51'18"W	39.1 m	NDBC
St.John	St. John NB, Bay of Fundy	Land Station	45°19'05"N	65°53'08"W	108.8 m	DFO

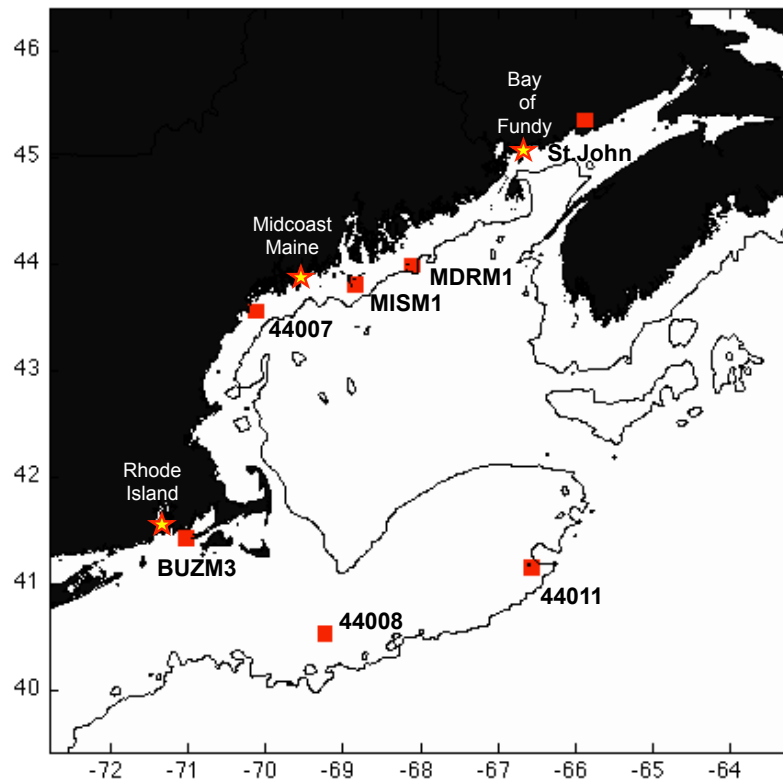


Figure 4. Location of buoys and land stations providing wind data for this analysis (red boxes). Stars show lobster settlement study regions. Black contour represents the 100m isobath. The three closest stations to each lobster settlement index region were used in the wind correlation analysis (Bay of Fundy: St. John, MDRM1 & MISM1; Midcoast Maine: 44007, MISM1 & MDRM1; Rhode Island: BUZM3, 44008 & 44011).

Separating the alongshore and cross-shore wind components runs the risk of missing wind signals that may be important to shoreward transport of lobster larvae due to their combined affect. To overcome this, I calculated the fraction of days wind blew in a direction favorable to onshore Ekman transport (from 65° to 155° from true North) on a monthly and seasonal basis. I term this the Coastal Wind Index (CWI) as it defined the fraction of days winds blew in onshore and alongshore directions favorable to shoreward transport of lobster larvae (Figure 7).

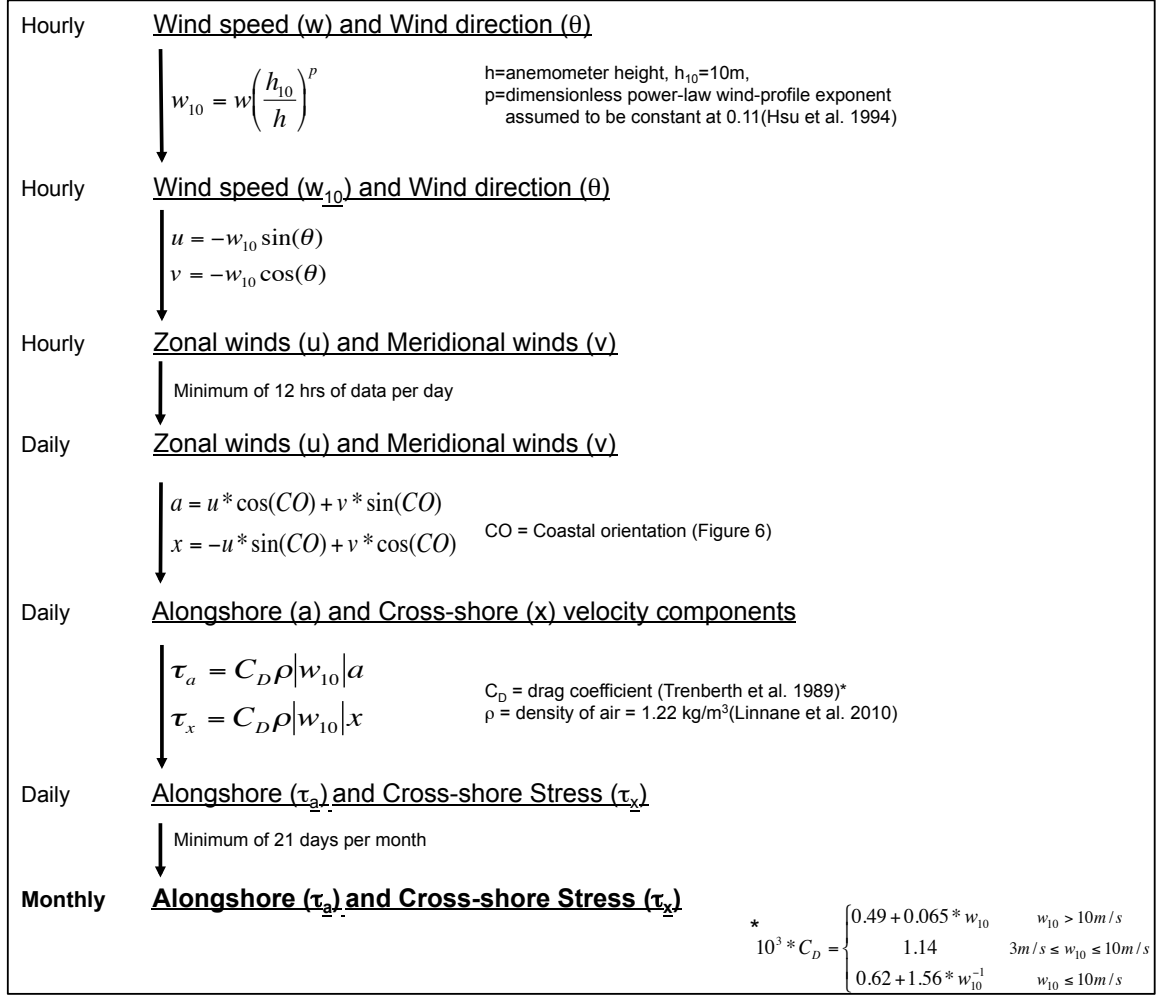


Figure 5. Flow chart of monthly average alongshore (τ_a in $N\ m^{-2}$) and cross-shore stress (τ_x in $N\ m^{-2}$) calculation from hourly wind speed (w in $m\ s^{-1}$) and direction (θ in degrees from true North).

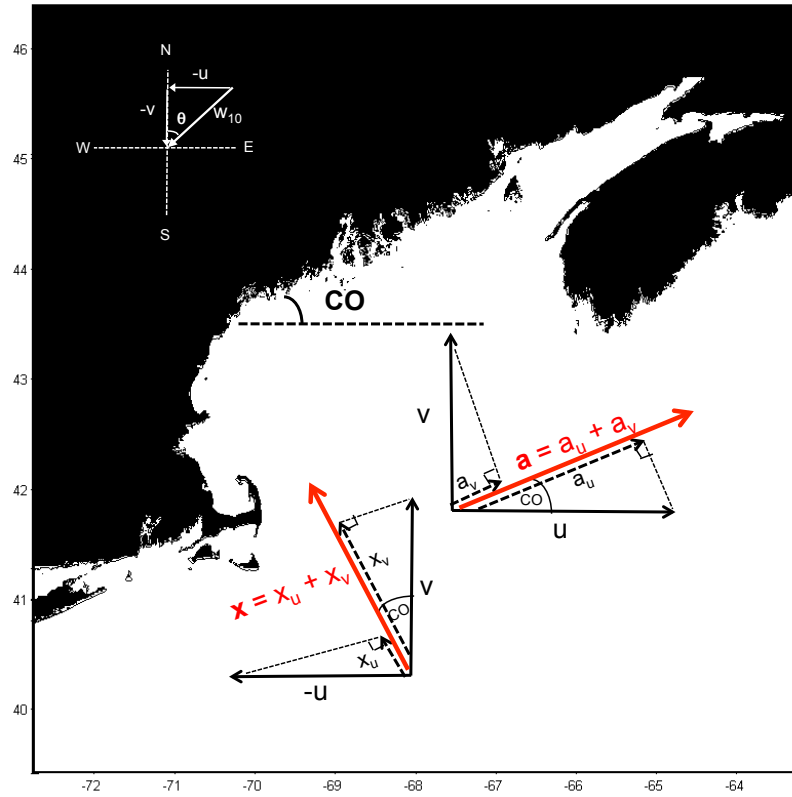


Figure 6. Vector diagrams showing the basis of alongshore (a) and cross-shore (x) wind speed derivation from u and v components with respect to the coastal orientation (CO, taken to be 25° anticlockwise from east for all sites). Diagram on top left corner shows the u and v components of wind speed (w_{10}) coming from θ degrees clockwise from true north.

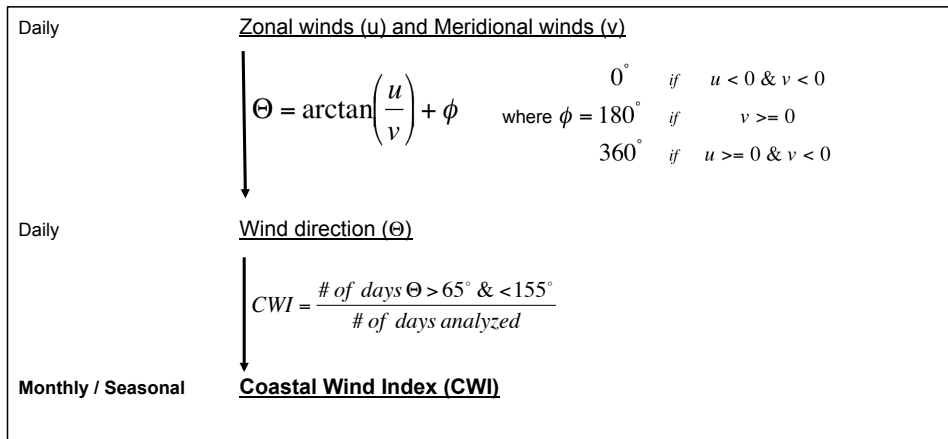


Figure 7. Flow chart of Coastal Wind Index calculation from daily u and v averages.

3.4 RIVER DISCHARGE

This study also evaluated the correlation of interannual lobster settlement with long-term river discharge records. Discharge data were available from the United States Geological Survey (USGS; <http://waterdata.usgs.gov/nwis>) and Water Survey of Canada (WSC; <http://www.wsc.ec.gc.ca/applications/H2O/index-eng.cfm>), which have long-term river gauge sites where data such as temperature, volume flux, flow level etc. are recorded on a daily (if not hourly) basis. Here I used monthly discharge data for the largest rivers ($> 100 \text{ m}^3 \text{ s}^{-1}$ monthly discharge) located within 100 km radius of the settlement region in question (Table 3, Figure 8). Average monthly volume flux ($\text{m}^3 \text{ s}^{-1}$) from Kennebec and Penobscot Rivers were combined for comparison to Midcoast Maine lobster settlement, as these rivers are highly correlated on an interannual basis (Thomas et al. 2010). Connecticut River was used for comparison to Rhode Island. Average monthly flow level (m above sea level) from St. John River was used for comparison to Bay of Fundy lobster data (Table 3, Figure 8).

Table 3. Details of river gauge stations and their data sets used in this study.

River	Location	Latitude	Longitude	Dams	Data Type	Source
St. John River	Fredericton, NB, Canada	45°57'58"N	66°39'5"W	No	Flow Level (m)	WSC
Penobscot River	West Enfield, ME, USA	45°14'10"N	68°39'05"W	Yes	Volume flux ($\text{m}^3 \text{ s}^{-1}$)	USGS
Kennebec River	Bingham, ME, USA	45°03'07"N	69°53'08"W	Yes	Volume flux ($\text{m}^3 \text{ s}^{-1}$)	USGS
Conneticut River	Thomsonville, CT, USA	41°59'14"N	72°36'21"W	No	Volume flux ($\text{m}^3 \text{ s}^{-1}$)	USGS

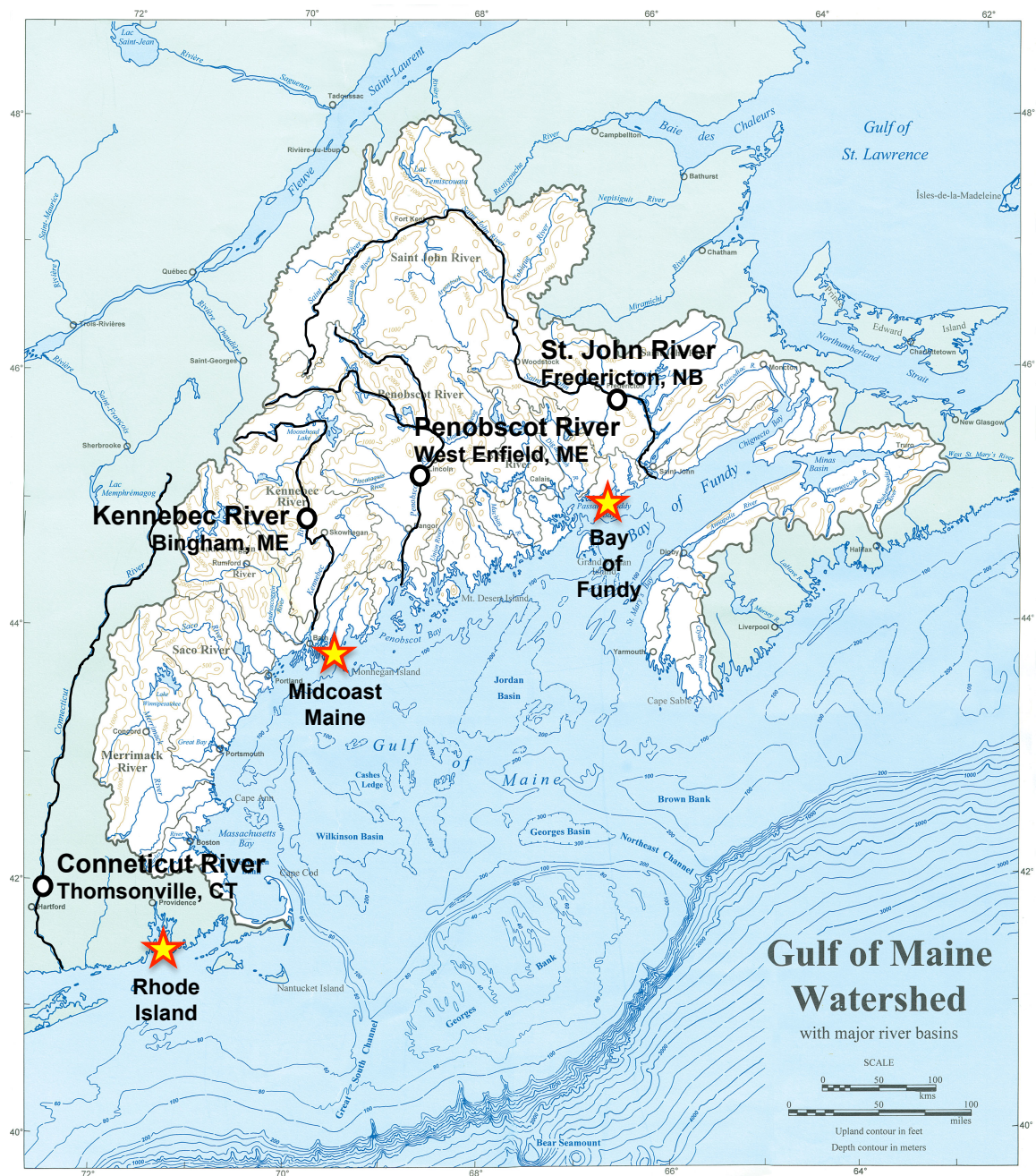


Figure 8. Major rivers draining near settlement regions (stars) and location of river gauge stations (circles). (Original Gulf of Maine Watershed map created by Richard D. Kelly, Jr., Maine State Planning Office, for the Gulf of Maine Council on the Marine Environment).

The Kennebec and Penobscot gauge stations with the longest river discharge time series were upstream of dams (Table 3, Figure 8) but showed strong correlations ($p < 0.001$) with downstream dam free sites (Appendix B). The St. John River flow level (m above sea level) correlated significantly ($p < 0.001$) to volume discharge (m^3s^{-1}) from a nearby gauge site (Appendix B). Thus both volume discharge and flow level irrespective of damming were valid indicators of freshwater discharge to coastal zones.

3.5 DETRENDING TIME SERIES

Because the focus of the study was to investigate relationships between environmental variables and interannual variability in lobster settlement, time series with significant long-term time trends needed to be detrended so as to avoid spurious correlations that may have arisen due to unresolved long-term temporal trends.

All individual data time series, except SSTa, were tested for significant temporal trends ($p < 0.05$). Time series with resultant significant trends were detrended prior to the correlation analysis. Because the use of the SSTa data involves correlating time series at each pixel location in the satellite image with the lobster settlement index, i.e. more than 3×10^5 correlations per analysis, it was easier to detrend the entire SSTa dataset than to search for and then only detrend SSTa pixels with significant time trends.

3.6 CORRELATION ANALYSIS

After detrending the time series with significant trends, monthly Spearman's rank correlations were performed between the annual lobster settlement time series and the environmental variables. This non-parametric correlation approach was used to avoid violating assumptions of parametric statistics, namely the normal distribution in the data sets and the linear co-variation between variables (Sokal and Rohlf, 1981). Correlations were conducted for the month of settlement sampling and up to three months prior to it, by negatively time lagging the monthly environmental variable.

For each monthly SSTa correlation analysis, the Spearman's rank correlation coefficient was calculated between the lobster settlement index for a region and the detrended monthly SSTa time series at each pixel location in the satellite image ($\sim 3 \times 10^5$ SSTa time series). For each monthly wind analysis, Spearman's rank correlations were calculated between the lobster settlement index for a region and the wind parameter at three of the closest meteorological recording stations (Figure 4). For each monthly river discharge analysis, Spearman's rank correlation was calculated between the settlement index for a region and the closest large river (Midcoast Maine used an average of Kennebec and Penobscot River discharges, Figure 8).

3.7 TEST FOR TYPE I STATISTICAL ERROR

Performing multiple SSTa correlations with a single data set (lobster settlement index) greatly increases the risk of falsely rejecting the null hypothesis, that is, detecting an association when there is none (Type I statistical error). Although a Bonferroni correction can help reduce this risk, it can increase the risk of a Type II error, the failure to observe an existing association. In order to distinguish actual from spurious correlations we devised a statistical test similar to the bootstrap technique used by Barton et al. (2003) and Thomas et al. (2010).

The bootstrap statistical test was performed for all lobster settlement – SSTa correlations to determine the risk of a Type I statistical error. In the bootstrap statistical tests, the lobster settlement time series was randomized and then the correlation was performed in a manner similar to the original analysis, this was repeated 100 times. From these 100 randomized resampling tests, the probability of spurious correlation was calculated as the fraction of times more pixels were significantly correlated ($p < 0.05$) than in the original analysis. If this probability of spurious correlations fell below 0.1, one was able to determine a significant association and reject the null hypothesis.

4. RESULTS

4.1 LONG TERM TRENDS IN LOBSTER SETTLEMENT

Long term increasing and decreasing trends are clearly visible for the Bay of Fundy and Rhode Island regions, respectively, whereas the Midcoast Maine time series has fluctuated over the period without any long-term trends (Figure 9). A significant ($p < 0.05$) increasing quadratic trend was observed in annual lobster settlement densities at the Bay of Fundy from 1991 to 2008. However, this quadratic trend was unable to fully account for the high settlement density observed in 2005 (Figure 9). Rhode Island, on the other hand, had a significant ($p < 0.05$) decreasing linear trend in lobster settlement as observed from 1990 to 2008 (Figure 9). There was no significant trend observed in the Midcoast Maine settlement index time series analyzed from 1989 to 2008. In all three cases there was considerable variability in settlement from year to year (Figure 9).

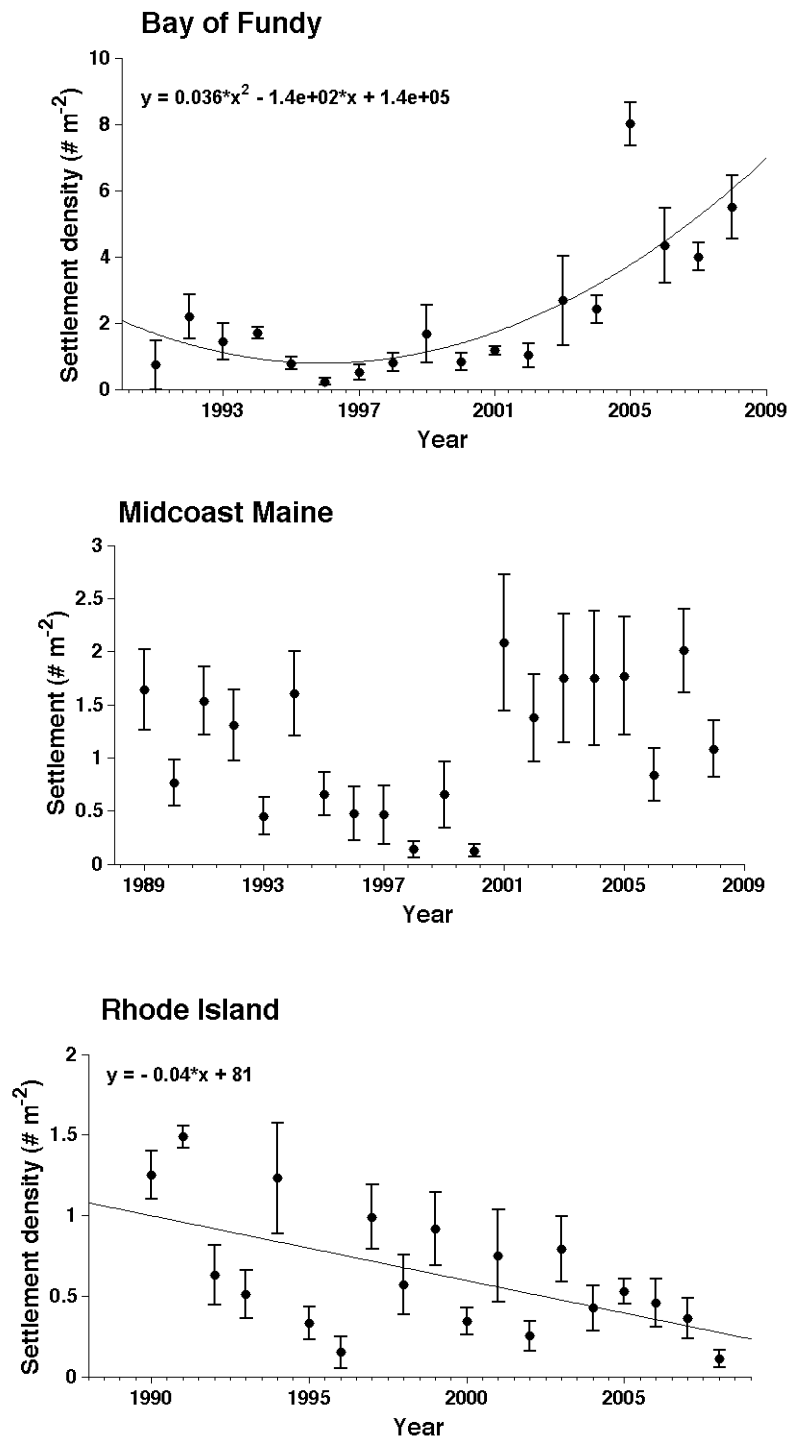


Figure 9. Average lobster settlement densities found in Bay of Fundy, Midcoast Maine and Rhode Island, showing significant time trends ($p < 0.05$) used to detrend the time series prior to correlating with environmental metrics. Error bars denote ± 1 Standard Error. (Source: American Lobster Settlement Index Collaborative).

4.2 LONG TERM TRENDS IN ENVIRONMENTAL METRICS

Of the time series of monthly wind and river discharge metrics analyzed only four showed significant ($p < 0.05$) long-term trends (Table 4). Significant linear trends in wind stress time series were found for alongshore stress at MISM1 in June and cross-shore stress at St. John in July (Table 4). Significant quadratic trends in river discharge time series were found for August in the Connecticut River and the Midcoast Maine (Kennebec and Penobscot Rivers) average (Table 4).

Table 4. Statistically significant ($p < 0.05$) trends in analyzed monthly wind and river discharge metric time series used to detrend the respective time series prior to correlating with the lobster settlement time series.

Environmental metric	Source	Month	t	Relationship	R ²
Alongshore stress	MISM1	June	1989-2008	$y = -7.5 \cdot 10^{-4}t + 1.52$	0.22
Cross-shore stress	St. John	July	1991-2008	$y = 1.9 \cdot 10^{-4}t + 0.38$	0.32
River volume flux	Midcoast Average	August	1989-2008	$y = 1.1t^2 - 4.4 \cdot 10^3t + 4 \cdot 10^6$	0.41
River volume flux	Connecticut River	August	1990-2008	$y = 3.27t^2 - 1.3 \cdot 10^4t + 1 \cdot 10^7$	0.3

4.3 RELATIONSHIP BETWEEN LOBSTER SETTLEMENT AND SEA SURFACE TEMPERATURE

The lobster settlement index in all regions significantly correlated with SSTa over a considerable area of the sea surface (Figure 10, 11 and 12). Although the areas and months that correlated with settlement differ from region to region, they generally

occurred during the months that larvae and postlarvae would be expected to occur in the water column.

At times we observed associations between the settlement index and SSTa off the continental shelf, outside the southern New England Shelf and Gulf of Maine, in the highly variable SST region near the Gulf Stream (Figure 10, 11 and 12). This area is dominated by variability from Gulf Stream flow, which varies in its location (being nearer or further off the shelf break) on an annual basis. High variability in Gulf Stream dynamics may have led to correlations with the settlement index at our inshore regions without there being an actual link between the two and thus should not be interpreted as an important source of settlement variability.

The Rhode Island lobster settlement index correlated positively with the SSTa primarily over Georges Bank for the months of June, July and August, but very little correlation was observed for the month of May (Figure 10). In addition to the region over Georges Bank, positive correlations were also observed in the Bay of Fundy and over southern New England Shelf, indicating that higher than average sea surface temperatures during June, July and August in these regions corresponded to higher settlement in Rhode Island (Figure 10). The bootstrap statistical test for Rhode Island showed that correlated areas as large as the ones observed in June, July and August, but not May, had a low probability ($p < 0.1$) of occurring by chance alone (Table 5).

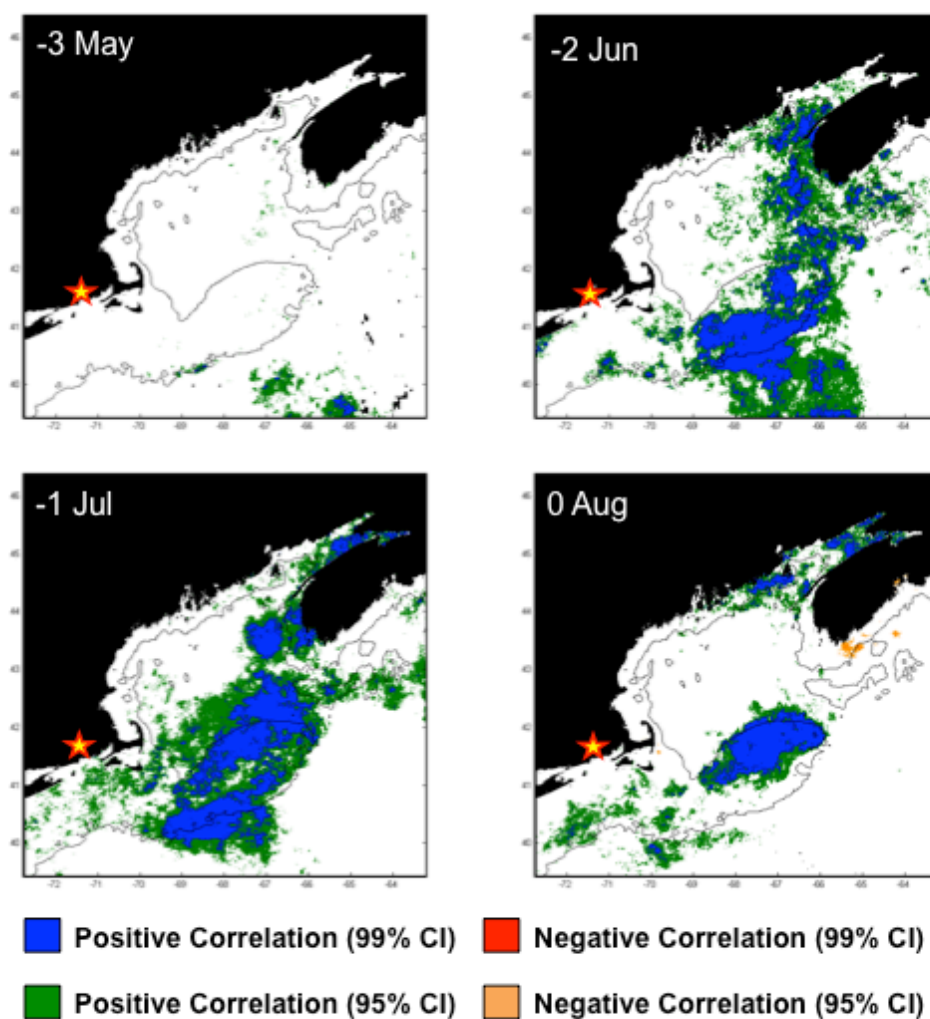


Figure 10. Rhode Island lobster settlement – SSTa correlation results. Areas of significant positive (blue and green) and negative (red and orange) correlations at two levels ($p < 0.01$ and $p < 0.05$) between the detrended Rhode Island (indicated by star) settlement time series and the detrended monthly SSTa pixels at negative time lags (-3 to 0 months) from when settlement is sampled in August. Black line indicates the 100 m isobath.

Table 5. Bootstrapping statistical test results for Rhode Island – SSTa correlation analysis.

Month	Time lag	Percentage of sea surface significantly correlated ($p < 0.05$)	Fraction of resampling tests exceeding original area
May	-3	2.2%	0.51
June	-2	32.9%	0.00
July	-1	33.2%	0.02
August	0	14.7%	0.10

The Midcoast Maine lobster settlement index correlated positively with SSTa in a small area just off the coast of Midcoast Maine and within the 100 m isobath during the month of September (Figure 11). Negative correlations were found between the patch over the Scotian Shelf and the settlement index for the month of August. No robust correlated areas were observed for June and July (Figure 11). Correlated areas of this size, however, could easily have occurred by chance (Table 6); thus the correlated regions observed in August and September should be interpreted with caution (Table 6, Figure 11).

The Bay of Fundy lobster settlement index was correlated with SSTa in patches offshore of and downstream from the settlement location site for each of the four months (Figure 12). Of these, however only the correlated areas in July and September were large enough to be unlikely to have occurred by chance (Table 7). These significant positive correlations in July and September indicate that higher than average SST in these areas corresponds to higher than average lobster settlement sampled in the Bay of Fundy region in the month of October (Figure 12).

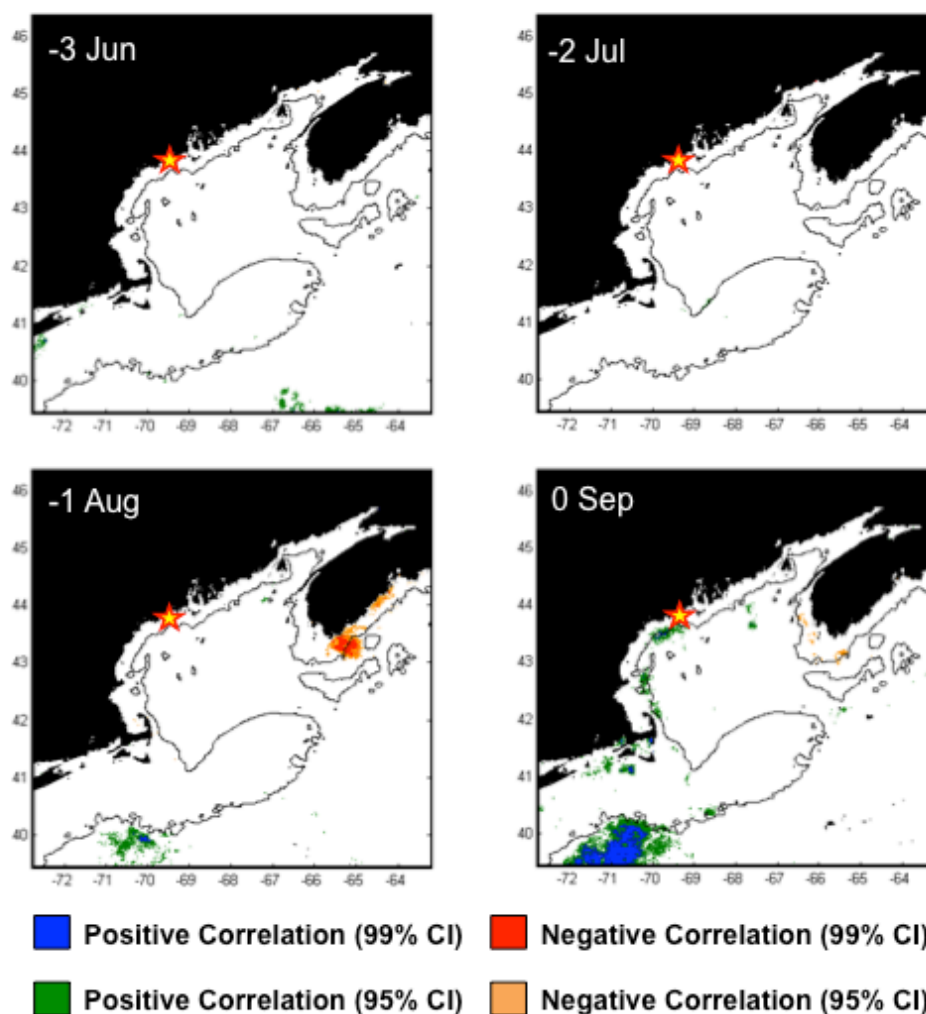


Figure 11. Midcoast Maine lobster settlement – SSTa correlation results. Areas of significant positive (blue and green) and negative (red and orange) correlations at two levels ($p < 0.01$ and $p < 0.05$) between the Midcoast Maine (red-yellow star) settlement time series and the detrended monthly SSTa images at negative time lags (-3 to 0 months). Black line shows the 100m isobath.

Table 6. Bootstrap statistical test results for Midcoast Maine – SSTa correlation analysis.

Month	Time lag	Percentage of sea surface significantly correlated ($p < 0.05$)	Fraction of resampling tests exceeding original area
June	-3	0.05%	0.88
July	-2	0.01%	0.97
August	-1	1.8%	0.61
September	0	4.6%	0.39

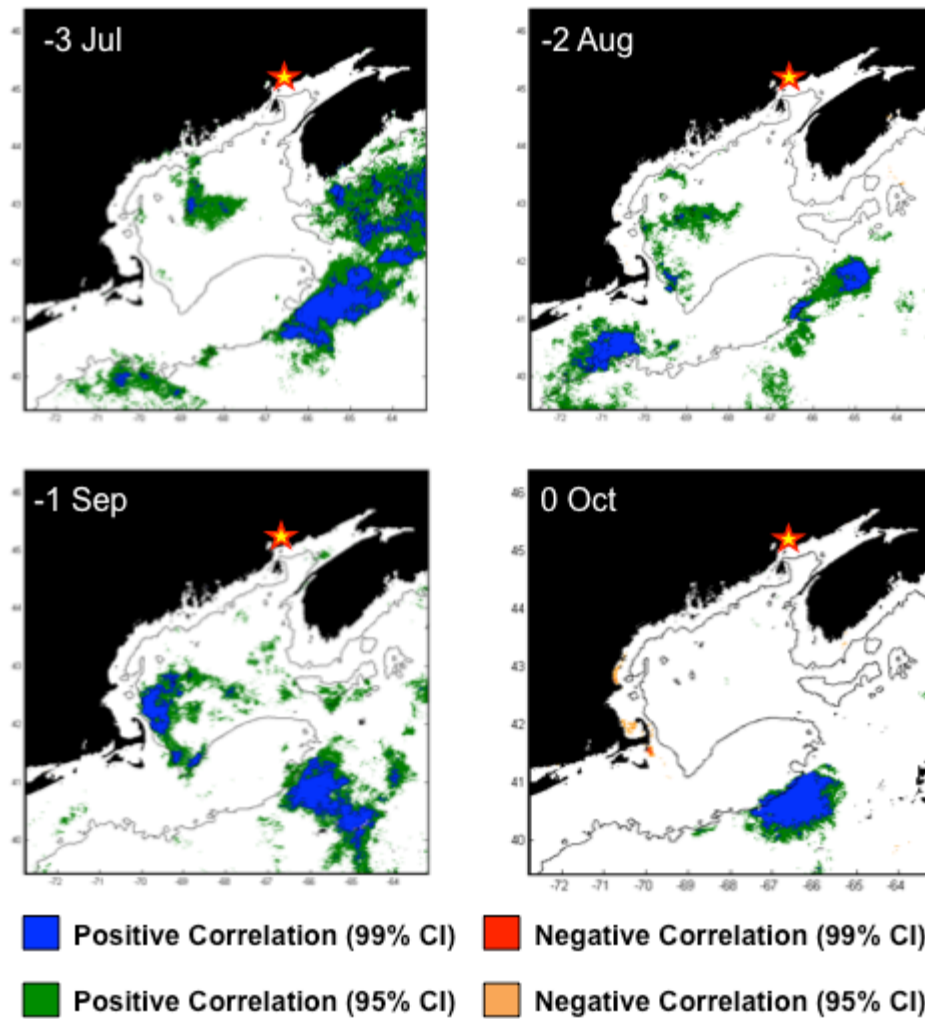


Figure 12. Bay of Fundy lobster settlement – SSTa correlation results. Areas of significant positive (blue and green) and negative (red and orange) correlations at two levels ($p < 0.01$ and $p < 0.05$) between the detrended Bay of Fundy (red-yellow star) settlement time series and the detrended monthly SSTa pixels at negative time lags (0 to -3 months) from when settlement is sampled. Black line indicates the 100m isobath.

Table 7. Bootstrap statistical test results for Bay of Fundy – SSTa correlation analysis.

Month	Time lag	Percentage of sea surface significantly correlated ($p < 0.05$)	Fraction of resampling tests exceeding original area
July	-3	20.7%	0.06
August	-2	11.4%	0.13
September	-1	13.8%	0.03
October	0	5.1%	0.33

4.4 RELATIONSHIP BETWEEN LOBSTER SETTLEMENT AND WIND

Monthly wind stress averages correlated significantly with the annual lobster settlement densities for all three lobster settlement sampling regions. In most cases significant correlations occurred one month prior to settlement sampling (Table 8).

Table 8. Wind stress correlation results. Spearman's rank correlation coefficients for relationship between settlement index data at specified regions and monthly wind stress (alongshore and cross-shore) averages at negative time lags of 3 to 0 months prior to settlement sampling. Highlighted cells show significant r-values. Rhode Island and Bay of Fundy lobster settlement time series were detrended in addition to the alongshore stress at MISM1 for June and cross-shore stress at St.John for July.

RHODE ISLAND

Alongshore Wind Stress				
Station	-3 May	-2 Jun	-1 Jul	0 Aug
BUZM3	0.04	-0.06	0.20	0.33
44008	0.09	0.09	-0.14	0.48
44011	0.10	0.10	0.16	0.52

Cross-shore Wind Stress				
Station	-3 May	-2 Jun	-1 Jul	0 Aug
BUZM3	0.14	-0.18	0.01	0.22
44008	0.14	-0.14	0.19	0.38
44011	0.15	-0.15	0.01	0.27

MIDCOAST MAINE

Alongshore Wind Stress				
Station	-3 Jun	-2 Jul	-1 Aug	0 Sep
44007	-0.09	-0.17	0.26	-0.30
MDRM1	-0.08	0.04	0.61	-0.04
MISM1	0.14	-0.34	0.38	-0.10

Cross-shore Wind Stress				
Station	-3 Jun	-2 Jul	-1 Aug	0 Sep
44007	-0.30	-0.04	0.28	0.12
MDRM1	-0.16	0.15	0.34	-0.01
MISM1	-0.21	0.08	0.44	0.00

BAY OF FUNDY

Alongshore Wind Stress				
Station	-3 Jul	-2 Aug	-1 Sep	0 Oct
St.John	-0.04	0.00	0.02	0.18
MDRM1	-0.09	-0.10	-0.02	0.29
MISM1	0.09	0.02	-0.05	0.28

Cross-shore Wind Stress				
Station	-3 Jul	-2 Aug	-1 Sep	0 Oct
St.John	-0.01	-0.02	0.68	0.19
MDRM1	0.13	0.23	0.48	0.04
MISM1	0.15	0.16	0.39	-0.13

Color Codes: p<0.05 p<0.1

The Rhode Island settlement index correlated significantly with alongshore wind stress (wind stress from the southwest direction) at the two buoys over Georges Bank for August, the month of settlement sampling (Table 8). The positive correlation indicates that enhanced alongshore stress from the southwest direction over Georges Bank related to higher settlement in Rhode Island for the month of settlement sampling. Although the relationship was positive, the lack of significance with the Buzzards Bay (BUZM3) buoy may be due to four missing years in that time series (Table 8). The Rhode Island settlement index did not correlate with the coastal wind index, that is, the fraction of days wind blew in a direction favorable to onshore transport, at any location and for any of the months analyzed (Table 9).

The Midcoast Maine settlement index correlated significantly with alongshore wind stress in two out of the three wind data locations for the month of August, that is one month prior to settlement sampling (Table 8). This indicates that higher alongshore stress (enhancement of prevailing southwest winds) during August is associated with higher settlement in the Midcoast Maine sampled in September. Additionally the Midcoast Maine settlement also correlated significantly with cross-shore wind stress (stress from the southeast direction) at MISM1 during the month of August (Table 8). Correlations between Midcoast Maine settlement and wind stress only occurred in August, one month before settlement sampling. Midcoast Maine settlement correlated negatively with the coastal wind index, the fraction of days wind blew in a direction favorable to onshore transport, at one of the three stations for the month of September (Table 9).

Table 9. Coastal wind index correlation results. Spearman's rank correlation coefficients for relationship between settlement index data at specified regions and the monthly and seasonal coastal wind index (fraction of days with wind direction favorable for onshore larval transport) at negative time lags of 3 to 0 months prior to settlement sampling. Rhode Island and Bay of Fundy lobster settlement time series were detrended.

RHODE ISLAND

Station	-3 May	-2 Jun	-1 Jul	0 Aug	Seasonal
BUZM3	0.28	0.19	-0.13	-0.37	-0.05
44008	-0.13	-0.24	-0.22	-0.12	-0.24
44011	0.31	-0.20	0.01	-0.05	-0.04

MIDCOAST MAINE

Station	-3 Jun	-2 Jul	-1 Aug	0 Sep	Seasonal
44007	-0.08	-0.10	-0.08	-0.30	-0.37
MDRM1	0.37	0.19	-0.06	-0.17	0.16
MISM1	0.05	0.01	0.00	-0.42	-0.10

BAY OF FUNDY

Station	-3 Jul	-2 Aug	-1 Sep	0 Oct	Seasonal
St.John	0.07	-0.19	0.13	-0.38	-0.14
MDRM1	-0.12	-0.03	0.42	-0.36	-0.11
MISM1	-0.33	0.29	0.48	-0.42	-0.01

Color Codes: p<0.05 p<0.1

Lobster settlement in the Bay of Fundy in contrast, was positively correlated with cross-shore wind stress (wind stress from the southeast direction) at two of the three wind stations for the month of September (Table 8). Correlation coefficients were highest for the stations closest to the settlement site, and this association was only observed for September, that is one month prior to settlement sampling (Table 8). These significant positive correlations indicate that enhanced cross-shore stress from the southeast in the month of September is related to higher lobster settlement sampled in the month October in the Bay of Fundy. Bay of Fundy lobster settlement also correlated significantly with

the September coastal wind index at two of the stations, but not at the station closest to the settlement region (Table 9).

4.5 RELATIONSHIP BETWEEN LOBSTER SETTLEMENT AND RIVER DISCHARGE

The relationship between lobster settlement and river discharge was negative in most cases (Table 10). Only in the case of Midcoast Maine, however did the relationship approach even a marginally significant level ($p=0.09$). That is, when July discharge for Kennebec and Penobscot River was low, subsequent settlement sampled in September in Midcoast Maine tended to be high.

Table 10. River discharge correlation results. Spearman's rank correlation coefficients for relationship between settlement index data at specified regions and monthly river discharge averages at negative time lags of 3 to 0 months prior to settlement sampling. Highlighted cells show significant r values. Rhode Island and Bay of Fundy lobster settlement time series were detrended in addition to the August river discharge time series for the Connecticut River and the Midcoast Maine river average.

Region	River	Discharge	-3	-2	-1	0
Rhode Island	Connecticut River	Volume flux (m^3/s)	0.08	-0.19	-0.18	0.00
Midcoast Maine	Kennebec & Penobscot Average	Volume flux (m^3/s)	-0.18	-0.39	-0.02	-0.04
Bay of Fundy	St. John River	Flow Level (m)	-0.08	-0.06	-0.06	0.31

Color Codes: $p<0.05$ $p<0.1$

5. DISCUSSION

The focus of this study was to determine environmental correlates of interannual variability in American lobster settlement. Interannual variability in lobster settlement correlated strongly with SSTa and wind stress, but exhibited a weak association with river discharge. Significant monthly correlations with lobster settlement occurred during the time period relevant to lobster larval transport and settlement (0 to 2 months prior to settlement sampling).

Variability in recruitment of commercially important lobster species has often been attributed to environmental factors. For example, associations between lobster settlement and sea surface temperature were inferred with appropriate time lags for the European lobster, *Homarus gammarus* (Sheehy and Bannister 2002). A direct relationship between coastal current SST and the Western Australian rock lobster (*Panulirus cygnus*) settlement in inshore nurseries was determined using spatially averaged satellite SST data (Caputi et al. 2001). Additionally, direct relationships between lobster settlement in inshore grounds and winds responsible for onshore Ekman transport have been observed for the Caribbean spiny lobster, *Panulirus argus* (Eggleston et al. 1998), the Western Australian rock lobster, *Panulirus cygnus* (Caputi et al. 2001) and the Southern Australian rock lobsters, *Jasus edwardsii* (Linnane et al. 2010).

5.1 LONG-TERM TRENDS IN LOBSTER SETTLEMENT

Although we did not analyze drivers of long-term trends in annual lobster settlement, the trends observed in the Rhode Island and Bay of Fundy lobster settlement index time series warrant further discussion (Figure 9). The Rhode Island settlement has declined dramatically since the late 1990s (Figure 9) in concert with steep declines in adult populations over the past decade (ASMFC 2009). These declines have been so significant, that a moratorium was being considered on the southern New England fishery during the summer of 2010 (ASMFC 2010). The onset and persistence of shell disease along with increasingly frequent episodes of stressfully warm temperatures and hypoxia in coastal waters are considered the most likely causes of the recent demise of southern New England lobsters (Wahle et al. 2009). The eastern Gulf of Maine and the Bay of Fundy, by contrast, have shown a rapid increase in lobster settlement (Figure 9). Harvests of adult lobsters have also increased dramatically in this region over the past decade. In both cases, the relationship between long-term trends in settlement may relate to changes in the region's egg production, and the relationship may be borne out by further investigation of time series in the abundance of reproductive female lobsters from state and federal trawl surveys or commercial catch data.

5.2 ENVIRONMENTAL CORRELATES OF INTERANNUAL VARIABILITY IN LOBSTER SETTLEMENT

Of the three variables tested, SSTa and wind stress revealed the most robust associations with annual fluctuations in regional lobster settlement indices. These associations occurred as much as two months prior to settlement sampling, when larvae are likely to be in the water column. Local river discharge exhibited a weakly negative correlation with settlement for only one of the three regions analyzed (Table 10).

The Rhode Island settlement index showed significant correlations with SSTa and alongshore wind stress (Figure 10 and Table 8). The correlation between the Rhode Island settlement index and SSTa over Georges Bank during the two months prior to the end of the settlement season is especially strong (Figure 10 and Table 5). However, the mechanism behind this correlation remains unclear. The waters over Georges Bank are well mixed due to tidal mixing. Resultant upwelling often leads to deep-water expression at the surface (Figure 3, Townsend et al. 2006, Brink et al. 2009). The SSTa correlation over Georges Bank therefore may be indicative of annual variability in bottom water temperature over the southern New England Shelf. It is possible that higher than average bottom temperatures on the southern New England Shelf, combined with stronger than average southwesterly winds, lead to higher than average settlement rates on its coast. A considerable fraction of southern New England's egg production occurs on Georges Bank and in the offshore canyons (ASMFC 2009). Lobster larval stage distributions in neustonic samples on a transect from the offshore canyons on the southwest margin of

Georges Bank to the inshore areas of the southern New England Shelf revealed a potential for offshore to inshore recruitment between these locations (Katz et al. 1995). Surface drifter studies confirm the likelihood of passive larval transport between Georges Bank and coastal southern New England Shelf taking anywhere from 2 to 9 weeks depending on the location of release of passive particles (Manning et al. 2009), a time period relevant to lobster larval development and thus transport. Moreover, lobsters from Georges Bank and southern New England Shelf are genetically homogeneous and have been distinguished from Gulf of Maine and Scotian populations (Kenchington et al. 2010). While the mechanism of the association needs to be more closely examined, it is not necessary to invoke larval connectivity between coastal Rhode Island and Georges Bank to demonstrate the evidently strong predictive relationship between SSTa there and lobster settlement in Rhode Island. Positive correlations between the Rhode Island lobster settlement index and alongshore wind stress over Georges Bank for the month of August may be driven by the same factor as the SSTa data over the same region.

The Midcoast Maine lobster settlement index showed weak correlations with SSTa and river discharge but strong correlations with local alongshore stress (Figure 11 and Table 8). Alongshore stress from the southwest in relation to the orientation of the coastline could enhance settlement to our sites in Midcoast Maine due to the short distance over which larval transport is likely to occur between hatching and settlement. Most egg production in this region occurs shoreward of the 50m isobath, just a few kilometers from shore, and often within coastal embayments. Moreover, postlarvae are neustonic and likely to be transported mostly by wind-driven currents. Thus opportunity to be steered

by Ekman transport is likely to be small in this region. Further, support for this hypothesis comes from small scale (<1km) differences in lobster postlarval settlement on two sides of an island in Maine, where Wahle and Incze (1997) found consistently higher settlement on the west-facing shore of the island that is subject to prevailing southwesterly winds during the summer. Furthermore, alongshore winds (winds from southwest direction) tend to reduce connectivity between the Eastern and Western Gulf of Maine Coastal Current (Pettigrew and Xue 2006), and thus may be favorable to local larval retention. The egg production in the Midcoast Maine region is the highest of any of the lobster producing zones in Maine, and circulation modeling suggests a high degree of local larval retention in this area (Incze et al. 2010). The patch of positive SSTa correlation in the month of September, although not significant (probability of spurious correlations < 0.4), maps to the area of the Western Maine Coastal Current, that would be warmer during years in which the cool Eastern Maine Coastal Current does not reach as far west (Figure 11). It is reasonable to think that settlement in the Midcoast Maine may benefit from a weakened Western Maine Coastal Current not only due to the favorable temperatures that prevail during thermal stratification (Figure 3), but also due to reduced advection away from the settlement sites, and this mechanism can be tested using larval transport modeling.

Interannual variability in lobster settlement in the lower Bay of Fundy was positively correlated with SSTa and cross-shore wind stress (Figure 12 and Table 8). Significant ($p < 0.05$) positive correlations between lobster settlement in the Bay of Fundy and cross-shore wind stress from the southeast during the month of September, one month prior to

settlement sampling, makes intuitive sense in terms of Ekman transport into the Bay. Stronger than average lobster settlement was associated with areas of warmer than average sea surface temperature in the western Gulf of Maine within a month or two of the end of the settlement season (Figure 12). The SSTa patch over the Scotian Shelf that correlated significantly with Bay of Fundy settlement in the month of July may be related to incoming Shelf Water and its impact on Gulf of Maine circulation (Bisagni and Smith 1998). Warmer temperatures may indicate a reduced inflow of the cold Scotian Shelf Water, which in turn can reduce the flow of the Coastal Current and may affect larval supply to the nursery ground in Bay of Fundy, especially if accompanied with cross-shore winds (winds from the southeast) that favor Ekman transport into the Bay.

SSTa correlations over the Gulf Stream area beyond the continental shelf with any of the three lobster settlement time series were not regarded as a source of settlement variability. The high variability in Gulf Stream dynamics produces correlated areas with the settlement index, but these are not likely to be associated with ocean features that are fixed in space, nor are they likely to have a direct influence on lobsters on the benthos or in the plankton. A refined analysis of correlations between lobster settlement and satellite-derived SSTa should exclude this area dominated by Gulf Stream variability for both the correlation analysis and the bootstrap statistical test.

The weak negative association between lobster settlement and river discharge was only observed for Midcoast Maine. It is possible the effect of river discharge is relatively weak and localized for the Gulf of Maine and southern New England compared to that

observed in the Gulf of Saint Lawrence, where river discharge is two orders of magnitude greater than any analyzed here (Sutcliffe 1972 and 1973). Sutcliffe (1973) observed positive correlation between lobster harvests in the Gulf of St Lawrence and river discharge 8 - 9 years earlier. He hypothesized the impact of increased nutrient supply during years of high St. Lawrence flow on the productivity of larval lobsters and was able to show a link between larval stage I production and local river discharge (Sutcliffe 1972).

It is important to note that there were no significant correlations three months prior to settlement sampling when larvae are not expected in the water column. The only exception to this generality was the association between Bay of Fundy lobster settlement and SSTa over the Scotian Shelf in July. Thus, most of the significant environmental correlates occurred for the months that are most relevant to lobster larval supply and transport.

This study is the first to examine environmental correlates of American lobster settlement in inshore nursery grounds on such large spatial and temporal scales. The use of satellite data has enabled us to determine oceanographic features important to lobster settlement. In short, sea surface temperature anomalies and wind stress proved to be strong environmental correlates of lobster settlement in this analysis, while local river discharge only provided weak associations. In all cases, statistically significant correlations occur at monthly time lags relevant to lobster larval transport and settlement.

6. CONCLUSIONS AND FUTURE RESEARCH

This study identified SSTa and wind stress as significant correlates of American lobster settlement in inshore nursery grounds. The exact relationships vary from site to site but there is consistency in timing of observed significant associations (within two months prior to the settlement sampling). Application of satellite SSTa data and wind data from multiple stations identified areas of the sea surface that may constitute important predictors of interannual variability. Because this analysis used settlement data up to 2008, predictive models of American lobster settlement that incorporate variability from SSTa and wind stress can be used to forecast settlement in 2009 and 2010 to test the relationships that emerge from this study. Further studies to understand the mechanisms behind observed associations will require augmented *in situ* pelagic larval sampling and or additional larval transport modeling.

This study is the first to examine large-scale spatial associations between satellite derived SSTa and lobster settlement. Our work supports the application of SST and wind data in biophysical models of larval transport. Once available, longer satellite wind time series warrant a test of the spatial association between inshore American lobster settlement and satellite-derived wind stress.

In conclusion, this study stresses the value in maintaining and sharing long-term biological and physical data sets. Oceanographic satellites provide a wealth of information that is otherwise impossible to achieve. Biological datasets, like the

American Lobster Settlement Index are important indicators of population health. Statistical exploration of the lobster settlement index from three important lobster producing regions has helped identify SSTa and wind stress as important correlates of interannual variability in lobster postlarval supply. And the potential for predicting interannual variability in lobster settlement based on these relationships can be very useful to fishery managers.

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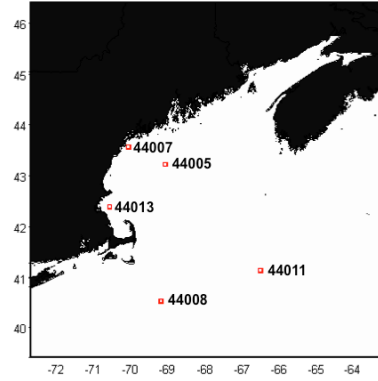
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APPENDIX A: SST VALIDATION

Satellite monthly SST vs. Buoy monthly SST averages. Buoys used in this analysis are 44005, 44007, 44008, 44011 and 44013 (Shown in image on right). Pearson's correlation results given below provide the r , p and n for each month the correlation was performed between the point source satellite data, 25 km² average (inner square in image) and 100 km² average (outer square in image) and the buoy data. Cells highlighted yellow show significant ($p < 0.05$) correlations.



	44005			44007			44008			44011			44013			All five		
	r	p	n	r	p	n	r	p	n	r	p	n	r	p	n	r	p	n
Jan	0.79	0.00	22	0.86	0.00	22	0.70	0.00	22	0.67	0.00	22	0.90	0.00	23	0.85	0.00	111
Feb	0.82	0.00	21	0.81	0.00	20	0.92	0.00	21	0.80	0.00	21	0.93	0.00	23	0.93	0.00	106
Mar	0.82	0.00	23	0.69	0.00	21	0.79	0.00	22	0.77	0.00	21	0.82	0.00	23	0.89	0.00	110
Apr	0.59	0.00	21	0.58	0.01	20	0.68	0.00	23	0.80	0.00	20	0.82	0.00	22	0.76	0.00	106
May	0.28	0.23	20	0.67	0.00	21	0.40	0.06	23	0.68	0.00	22	0.71	0.00	22	0.70	0.00	108
Jun	0.46	0.03	22	0.87	0.00	22	0.77	0.00	22	0.78	0.00	22	0.85	0.00	22	0.86	0.00	110
Jul	0.78	0.00	22	0.70	0.00	22	0.83	0.00	23	0.85	0.00	21	0.62	0.00	22	0.81	0.00	110
Aug	0.39	0.08	21	0.67	0.00	22	0.82	0.00	23	0.92	0.00	21	0.71	0.00	22	0.81	0.00	109
Sep	0.28	0.25	19	0.86	0.00	20	0.81	0.00	22	0.94	0.00	21	0.90	0.00	20	0.89	0.00	102
Oct	0.00	0.99	19	0.93	0.00	20	0.92	0.00	21	0.71	0.00	21	0.83	0.00	20	0.89	0.00	101
Nov	0.16	0.51	19	0.92	0.00	20	0.84	0.00	21	0.52	0.02	20	0.07	0.77	21	0.71	0.00	101
Dec	0.71	0.00	20	0.93	0.00	21	0.89	0.00	22	0.62	0.01	17	0.92	0.00	21	0.92	0.00	101

	44005 [25km ²]			44007 [25km ²]			44008 [25km ²]			44011 [25km ²]			44013 [25km ²]			All five [25km ²]		
	r	p	n	r	p	n	r	p	n	r	p	n	r	p	n	r	p	n
Jan	0.80	0.00	22	0.86	0.00	22	0.70	0.00	22	0.61	0.00	22	0.89	0.00	23	0.83	0.00	111
Feb	0.85	0.00	21	0.81	0.00	20	0.94	0.00	21	0.80	0.00	21	0.91	0.00	23	0.93	0.00	106
Mar	0.83	0.00	23	0.67	0.00	21	0.80	0.00	22	0.84	0.00	21	0.78	0.00	23	0.89	0.00	110
Apr	0.57	0.01	21	0.59	0.01	20	0.68	0.00	23	0.80	0.00	20	0.80	0.00	22	0.76	0.00	106
May	0.30	0.19	20	0.66	0.00	21	0.43	0.04	23	0.66	0.00	22	0.72	0.00	22	0.71	0.00	108
Jun	0.46	0.03	22	0.87	0.00	22	0.75	0.00	22	0.79	0.00	22	0.84	0.00	22	0.86	0.00	110
Jul	0.79	0.00	22	0.70	0.00	22	0.82	0.00	23	0.85	0.00	21	0.65	0.00	22	0.81	0.00	110
Aug	0.40	0.07	21	0.65	0.00	22	0.82	0.00	23	0.93	0.00	21	0.70	0.00	22	0.81	0.00	109
Sep	0.33	0.17	19	0.86	0.00	20	0.81	0.00	22	0.94	0.00	21	0.91	0.00	20	0.89	0.00	102
Oct	0.01	0.97	19	0.92	0.00	20	0.92	0.00	21	0.71	0.00	21	0.84	0.00	20	0.89	0.00	101
Nov	0.52	0.02	19	0.92	0.00	20	0.41	0.06	21	0.54	0.01	20	-0.19	0.41	21	0.73	0.00	101
Dec	0.72	0.00	20	0.94	0.00	21	0.89	0.00	22	0.61	0.01	17	0.92	0.00	21	0.92	0.00	101

	44005 [100km ²]			44007 [100km ²]			44008 [100km ²]			44011 [100km ²]			44013 [100km ²]			All five [100km ²]		
	r	p	n	r	p	n	r	p	n	r	p	n	r	p	n	r	p	n
Jan	0.80	0.00	22	0.88	0.00	22	0.73	0.00	22	0.59	0.00	22	0.89	0.00	23	0.83	0.00	111
Feb	0.87	0.00	21	0.80	0.00	20	0.93	0.00	21	0.83	0.00	21	0.91	0.00	23	0.94	0.00	106
Mar	0.83	0.00	23	0.66	0.00	21	0.78	0.00	22	0.83	0.00	21	0.77	0.00	23	0.89	0.00	110
Apr	0.58	0.01	21	0.58	0.01	20	0.68	0.00	23	0.81	0.00	20	0.81	0.00	22	0.76	0.00	106
May	0.32	0.17	20	0.65	0.00	21	0.42	0.05	23	0.64	0.00	22	0.73	0.00	22	0.71	0.00	108
Jun	0.46	0.03	22	0.89	0.00	22	0.78	0.00	22	0.80	0.00	22	0.85	0.00	22	0.86	0.00	110
Jul	0.80	0.00	22	0.71	0.00	22	0.83	0.00	23	0.85	0.00	21	0.67	0.00	22	0.81	0.00	110
Aug	0.40	0.07	21	0.64	0.00	22	0.84	0.00	23	0.94	0.00	21	0.68	0.00	22	0.82	0.00	109
Sep	0.32	0.18	19	0.86	0.00	20	0.82	0.00	22	0.95	0.00	21	0.92	0.00	20	0.90	0.00	102
Oct	0.00	0.99	19	0.90	0.00	20	0.93	0.00	21	0.73	0.00	21	0.84	0.00	20	0.89	0.00	101
Nov	0.41	0.08	19	0.92	0.00	20	0.49	0.02	21	0.55	0.01	20	-0.22	0.34	21	0.68	0.00	101
Dec	0.71	0.00	20	0.94	0.00	21	0.90	0.00	22	0.71	0.00	17	0.92	0.00	21	0.93	0.00	101

APPENDIX B: RIVER DISCHARGE VALIDATION

Pearson's Correlation results for River discharge time series to test the effects of damming (Kennebec and Penobscot Rivers) and the relationship between Level and Volume Flux data (St. John).

Kennebec River – Volume flux ($\text{m}^3 \text{s}^{-1}$) data was used from Bingham, ME, that is located above major dams. North Sidney volume flux data is free of damming post 1999. The analysis here uses data from 2000 – 2009.

Kennebec River (Bingham vs. North Sidney)

	Jun	Jul	Aug	Sep
r	0.89	0.98	1.00	0.92
p	0.00	0.00	0.00	0.00
n	10	10	10	10

Penobscot River - Volume flux ($\text{m}^3 \text{s}^{-1}$) data was used from West Enfield, ME, that is located above major dams. Eddington ME is dam free volume flux site. The analysis uses data from 1979 – 1996.

Penobscot River (West Enfield vs. Eddington)

	Jun	Jul	Aug	Sep
r	1.00	1.00	0.99	1.00
p	0.00	0.00	0.00	0.00
n	18	18	18	18

St. John River – Level (m above sealevel) data was used from Fredericton, NB. Flow data ($\text{m}^3 \text{s}^{-1}$) from below Mactaquac, NB is used here to test the relationship between the two variables. Both sites are dam free. The analysis uses data from 1967-1994.

St. John River (Fredericton vs. Mactaquac)

	Jul	Aug	Sep	Oct
r	0.98	0.98	0.99	0.98
p	0.00	0.00	0.00	0.00
n	26	26	27	27

BIOGRAPHY OF THE AUTHOR

Mahima Jaini was born in New Delhi, India on March 25th 1986. She graduated from Carmel Convent School, New Delhi, India, in 2003. After high school Mahima pursued a year of zoology at Hindu College, Delhi University before moving to the United States for studies in marine biology. Mahima graduated from the University of Maine with a Bachelor of Science degree in Marine Sciences and a minor in fisheries in May of 2008. She is a candidate for the Master of Science degree in Marine Biology from the University of Maine in May, 2011.